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Fish body sizes change with temperature, but not all species shrink with warming

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Summary

Ectotherms generally shrink under experimental warming, but whether this pattern extends to wild populations is uncertain. We analysed ten million visual survey records, spanning the Australian continent, multiple decades and comprising all common coastal reef fish (335 species). We found that temperature indeed drives spatial and temporal changes in fish body size, but not consistently in the negative fashion expected. Around 55% of species were smaller in warmer waters (especially among small-bodied species) while 45% were bigger. The direction of a species' response to temperature through space was generally consistent with its response to temperature increase at any given location, suggesting that spatial trends could help forecast fish responses to warming. However, temporal changes were ~10x faster than spatial trends (~4% versus ~40% body size change per 1°C change through space and time respectively). The rapid and variable responses of

fish sizes to warming may herald unexpected impacts on ecosystem restructure, with potentially greater consequences than if all species were shrinking.

One sentence summary (125 characters): Spatial relationships between fish body size and temperature can help predict responses to warming through time

Main

Body size is a key biological and ecological trait [1,2], but many natural populations have undergone declines in average body size due to harvesting, with consequent reductions in ecosystem functional diversity and resilience [3-5]. More equivocal are declines in ectotherm body size caused by increased temperature, even though such declines are considered a third universal response to global warming [6], and, unlike harvesting, act on all species in an ecosystem. While some models forecast a 15-30% decrease in body sizes due to warming by 2050 [7,8], the generality of these responses remains debated on the theoretical basis [9] and in the light of some empirical observations [10]. Within species, smaller adult body sizes at warmer temperatures are commonly found under experimental conditions, having been observed in animals as diverse as insects, worms, reptiles and fishes[11]. Nevertheless, the mechanisms and adaptive significance of this phenomenon, often described as a temperature-size rule, remain elusive and controversial since Bergman's publication in 1847 [11-13]. Experimental temperature-size responses are particularly apparent for aquatic species, a pattern that has spawned hotly debated hypotheses on the role of oxygen supply [14-16]. For example, an average adult body weight decrease of 5% per 1°C of warming was observed across 169 aquatic species, versus just 0.5% decrease in terrestrial taxa [14]. Yet, the applicability of experimental studies to wild populations remains questionable, because few experiments have explored body size responses through multiple generations where intergenerational plasticity and rapid adaptations are likely to alter the observed responses[17]. Moreover, the realised size in wild populations integrates growth, recruitment, mortality, competition, predation risk and food availability simultaneously, and the interplay of these factors

cannot be adequately addressed in experiments[10].

Climate change ecology has thus far largely focused on shifting geographic distributions, phenology and abundance of organisms, and the consequences of these [18], whereas warming-driven changes in body sizes across a broad range of species (both unexploited and exploited) have not been systematically assessed. This study capitalises on large underwater visual survey datasets from the National Reef Monitoring Network in Australia (consisting of the Australian Temperate Reef Collaboration (https://atrc.org.au/) and Reef Life Survey (https://reeflifesurvey.com/)[19,20]. The datasets consist of >30,000 surveys of rocky and coral reefs around the Australian continent (Extended Data Fig. 1), where abundance and sizes of all fish species along standardised transects is recorded by trained divers. Some locations have been continuously monitored for over 26 years. From these surveys we selected all fish species that satisfied the minimum abundance and occurrence frequency criteria, resulting in 335 common coastal species spanning a range of maximum body size and life-history characteristics. Majority of these species (254 out of 335) are unlikely to be targeted by fishing in the study region, and only 42 species are known to be commonly caught by recreational or commercial fishers (the remaining 39 species could be occasionally caught, but fishing mortality is likely to be low, see Supplementary Information Table 1). We then use Bayesian methods to fit hierarchical, mixed-effects models that account for random errors in space and time to quantify spatial and temporal relations between mean individual body length and temperature or time.

Results

In the first set of analyses, species' mean annual body length was assessed against the annual mean sea surface temperature (SST) at locations spanning their distributions. Approximately half of the species showed clear trends in body size with temperature (for which lower or upper 10% of the posterior probability density or PPD range of the size-SST slope was above or below zero

77 respectively), with 97 species declining in size towards the warmer edge of their distribution, and 64
78 species increasing (Fig. 1A, Supplementary Information Table 2). Fish species included in our study
79 grouped into two major thermal guilds [21], corresponding to temperate and tropical distribution types.
80 In our analyses, temperate species constituted about a third of the total species analysed and were
81 equally likely to have negative or positive body size responses to temperature (Fig. 1A,
82 Supplementary Information Table 2). In contrast, tropical species were twice as likely to be smaller
83 than larger at their warm distribution edge (see Supplementary Information Table 1 showing the list
84 of species and their individual body size responses to temperature). In addition, relative change in
85 species' mean body length was, on average, positively related to the maximum body length (Fig.
86 1B), meaning that small-bodied species tended to be smaller in warmer areas and larger species
87 tended to be larger. This contradicts experimental temperature-size observations, where strongest
88 declines in adult body sizes occurred in largest species [14] and where oxygen supply was suggested as
89 playing a critical role. Given that small individuals are more likely to be overestimated in size by
90 divers undertaking surveys (due to inherent and consistent biases in diver perceptions of sizes
91 underwater [22]), our result is likely conservative. Notably, body size-temperature trends in space were
92 most often linear, or at least not strongly curved, suggesting that for most species there was not an
93 "optimal" temperature in the central part of the distribution range at which body size was maximised
94 (Supplementary Information Fig. 1). Density-dependent processes, such as abundance skew statistics
95 across species distribution ranges [23], did not appear to explain the observed size trends either (see
96 Methods and Extended Data Fig. 2).
97
98 While the spatial analyses ascertained length-temperature relations across many species'
99 distributions, we sought further evidence that these body size changes related specifically to
100 temperature by quantifying intra-specific changes in mean body length over time for all common fish
101 species at nine sites monitored for 15 to 26 years. Specifically, we estimated temporal trends in body
102 size for 105 species; of these 77 species were found at eight locations that have warmed significantly

over the time of observations (average trend of 0.025°C per year). Clear temporal changes in body size (90% PPD outside zero) were seen in more than half of the studied fish species (40 out of 77) in these warming locations (Supplementary Information Table 2), and from these, most (36 out of 40) were consistently decreasing or increasing in sizes across different, geographically distant locations. No significant linear long-term warming trend was observed in one of the monitored locations in Western Australia (Jurien Bay, Supplementary Information Table 3, Extended Data Figs. 1, 3) and this location also had the smallest proportion of species with temporal trends in body size (Supplementary Information Table 3). Some of the fastest rates of warming were observed in the southernmost locations in Tasmania, where 50-66% of species showed clear changes in body size through time. The correlation between the rate of warming and the number of species changing in size was weaker closer to the tropics (Jervis Bay site), where, despite the fast warming, only a third of species were clearly increasing or decreasing in size. Importantly, for species that were included in both spatial and temporal analyses (71 species), long-term rates of change in body length at the eight warming locations were positively correlated with the relative change in body length observed across the temperature gradient in space (Fig 2). In other words, species that were smaller at the warmer edge of their geographical distribution were also more likely to become smaller in locations that are warming, and vice-versa.

The two sets of analyses strongly suggest that temperature is a major determinant of reef fish body sizes in the wild, and that the magnitude of average body size change across space and time can be surprisingly large (Fig. 2, Extended data Fig. 3). For example, for species that showed clear body size changes with temperature through space (90% PPD outside zero, Fig. 1, constituting about half of all species), mean body length changed by ~4% for each degree of warming throughout their distribution (Supplementary Information Tables 1, 2). For a median length temperate fish (15 cm) with a typical body shape, this change in length corresponds to approximately 12% change in body mass per 1°C, and nearly a three-fold difference in mean mass between the equatorial and poleward

range of an average species distribution (8°C of annual SST range, giving 12 cm and 32 g versus 17 cm and 89 g on the extreme temperature ranges across the distribution, see Supplementary Information Table 2). Temporal changes in body size were even greater, averaging roughly 1% change in length per year in the 40 clearly changing species (90% PPD outside zero). If the rate of body size change and warming observed over the last 20 years was maintained, then 1^{o}C of warming predicted over the next 40 years would result in ~ 40% change (either increase or decrease) in fish body length. This means that body size responses to 1^{o}C temperature change through time were about ten times faster than those seen through space (depicted with the orange line in Fig. 2). The result was similar if the space-time comparison was constrained to species for which both temporal and spatial data was available (for these species the average change through space was ~3.5% for each degree of warming).

Several alternative explanations exist for the different rates of response to temperature gradients in space and time. First, rapid warming in time also leads to species redistributions and changing species interactions may accentuate emergent body size changes through time. Second, rapid warming is also likely to coincide with changes in productivity and changes in the growing season itself, which again is likely to magnify changes in body sizes observed in the field. Third, species are adapted to the local temperature range, more so than to temperatures experienced across their full distributional range, and are consequently sensitive to relatively slight temperature changes in the local environment[24]. Fourth, size patterns through space have emerged over many generations and likely involve adaptations that may reduce the temperature effects on growth. Counter-gradient variation, or opposite influences of genetic and environmental factors on phenotypes, has been detected in dozens of fish species and often involve changes in physiological rates that dampen the effects of temperature [25]. Presumably, rapid warming over the last two decades would not have allowed for the sufficient time for such adaptations to emerge. Nevertheless, even though the observed temporal rates of change are high, they are comparable to the rates of growth or maturation

change reported in harvested fish species (ca 0.5-4% per year) and smaller than evolutionary change in size under strong selection experiments (2-17% per year) [26].

Discussion

Our study provides strong empirical support for the differential effects of warming on body sizes of many common coastal marine fishes. Until now, the majority of size trend information for marine species was only available from commercially harvested or charismatic species, where effects of harvesting and warming are difficult to separate [27]. In our study, the effects of exploitation on body size are unlikely to affect overall conclusions because the number of commercially or recreationally fished species is small relative to the number of unexploited fish species inhabiting the shallow reefs surveyed, and because the temporal body size - temperature correlations inside and outside no-take marine protected areas were broadly similar (Supplementary Information Fig. 2). Species that showed the largest responses of body size to temperature represent useful priorities for further study to understand the underlying drivers, such as growth, mortality, recruitment, food availability and other demographic changes. Future work is also needed to disentangle the multiple ecological mechanisms and environmental stressors at play, as well as potential feedbacks. For example, how do warming-driven species redistributions interact with changes in body sizes? And what are the main reasons for different rates of responses through space and time?

Differential responses of species' body size to warming have implications for the restructuring of food webs and ecosystems, with consequences for the stability and resilience of local communities to other external stressors, such as fishing, coastal pollution, and the multi-faceted effects of climate change. Many biological functions scale allometrically with body size, hence the mean, variance, and shape of body size distributions within a community all influence aggregate ecosystem functioning [28]. Modelling studies show that even small changes in species body sizes, such as 4% decrease over

50 years could lead to increased mortality and up to 30% decrease in biomasses and productivity [29,30], yet the body size changes of common species in warming locations are often much greater (Extended Data Fig. 3). Of particular consequence is our finding that body size changes across the community are not proportionate across species – total biomass and production of larger predatory species are likely to increase with rising temperatures whereas production of small bodied prey species will decline. Complex changes to food web structure can thus be expected. Understanding how such body size trends might change functional roles of dominant species in marine ecosystems should be one of the top priorities for management and protection of marine biodiversity in a rapidly changing ocean.

Methods

Reef fish data

The study is based on up to 26 years of underwater surveys from around Australian continent and includes around 10 million observations of 335 fish species from around 30000 surveys. Data were obtained from standardised quantitative censuses of fishes undertaken as part of the Australian Temperate Reef Collaboration (ATRC) monitoring program conducted from 1992 to present, and Reef Life Survey (RLS) program from 2008 to present. The RLS program was developed based on the ATRC program, and the two approaches use consistent methodology other than extent of replication. Full details of fish census methods are provided in [19,20] and an online methods manual (http://www.reeflifesurvey.com) describes the different data collection methods. To maximise consistency in this study, we only used data from Method 1 surveys. These surveys involve divers laying 50 m transect lines and recording all fish species present within duplicate 5 m wide blocks (total area = 500 m^2), tallying abundance in size classes as the divers move along the transect. Fish sizes are recorded in $K = 28$ size (length) bin categories, with bin widths ranging from 2.5 cm for fish lengths below 15 cm, 5 cm for fish lengths between 15 and 40 cm, then 12.5 cm bins for fish lengths

over 50 cm. Data quality and training of divers are detailed in [20,31]. ATRC data are only collected by professional marine scientists with field experience, while the RLS data were collected by selected, trained and experienced recreational divers, who were each provided one-on-one training and calibration with experienced scientists before contributing data to the database. The data collected by these trained RLS volunteers has been formally evaluated and found to be indistinguishable from those of professional scientists at the same time and place [31].

Temperature data

For the spatial analyses, we grouped all fish survey sites into half a degree grid cells, resulting in 280 cells spanning mean annual sea surface temperature (SST) from 12°C to 29°C (Extended Data Fig. 1). For each of these cells we then extracted mean yearly SST values using daily temperature records from the NOAA Optimum Interpolation 1/4 Degree Daily Sea Surface Temperature model data [32] from 1982 until the end of 2018. Alternative temperature metrics (such as growth degree days, i.e. days with temperature above 12°C, or mean annual SST in previous years) gave overall similar results. Long-term annual change in SST was also estimated for nine locations using monthly average SST values, and accounting for a sinusoidal component of seasonal temperature variation. For each location mean SST at time *t* was described by: $\mu(t) = \beta_0 + \beta_1 t + \beta_2 \cos(2\pi(t - \phi))$, where *t* is years since January 1, 1982. Variation in observed SST about this mean was assumed to be normally distributed with fixed standard deviation, σ. All parameters were estimated using Bayesian methods and the resulting long term rates of change, given by β_1, are presented in the Supplementary Information Table 2 (analysis code available on https://github.com/astaaudzi/RLSfishSize).

Data filtering and selection

Reef fish size data were assessed for outliers and possible taxonomic errors by: i) filtering out observations in cells above and below 97.5% and 2.5% of the species distribution temperature (~1% of records) and ii) removing records that were 1.5 times larger than maximum species size known in

FishBase (a larger cut-off was used because reported maximum size in FishBase is smaller than the true maximum size for many unexploited species with limited life-history data) (~1.5% of records). To ensure enough data and statistical power to infer body size responses and account for random annual and spatial variation, the dataset used in the spatial analyses was restricted to taxa identified to species level, and only species containing at least 1000 individuals occurring in at least 10 geographic cells and over at least 5 years (e.g. a species with 1000 individuals observed in a single geographic cell or only recorded in 3 years was not used). We also excluded the smallest species that had maximum body sizes below 10 cm, because their data spanned too few size bins to discriminate trends. This gave 335 fish and shark species, across a range of temperature preferences and life-history strategies. To reduce the effect of recruitment pulses and vagrant recruits occurring outside species' normal distribution limits on estimates of body size - temperature responses, we removed observations below the 10^{th} percentile of the annual observed species body length (annual rather than one overall length was used to allow for the body size trends) (~3% of observations). While out-of-range observations may be important indicators of redistributions, we were interested in temperature – body size responses over the core ranges occupied consistently by species. The possible effects of this exclusion procedure on the conclusions from the hierarchical models (Fig.1A) were tested by repeating spatial analyses using all data from 10 small and 10 large species; we found that data exclusion did not affect the main conclusion (Supplementary Information Fig. 3). Temporal analyses were restricted to locations where surveys spanned at least 15 years with at least 10 annual surveys conducted in total. This left nine locations (Extended Data Fig. 1), each with an average of 44 sites repeatedly monitored (Supplementary Information Table 2). To improve estimates of temporal trends and associated random temporal errors, we restricted temporal analyses to species/location combinations where at least 20 individuals of a given species were observed per year at a location and at least 8 years of such observations were available (a species that was common for 5 years, but then fewer than 20 individuals observed per year in later years was not used, and likewise a location that was only sampled in e.g. 1992, 2000 and 2015 was not used).

259

260 **Statistical analyses**

261 The association between SST and the distribution of observed body sizes across a species' range was
262 quantified using a hierarchical, mixed-effect model. We assumed that observed log-transformed fish
263 lengths were drawn from a normal distribution with standard deviation, σ_{lnlength}, which was constant
264 across all surveys but differed among species. Size distributions within one species generally
265 followed a lognormal distribution (Supplementary Information Fig. 4). For survey *i* the mean of this
266 distribution is given by:

267

268 $$\mu_i = \beta_0 + \beta_1 x_i + \alpha_{\text{cell}[i]} + \alpha_{\text{year}[i]} + \alpha_i,$$

269

270 where μ_i is the ln transformed body length, x_i is the normalised mean annual SST in the cell, and β_0
271 and β_1 are species-specific regression coefficients to be estimated. We normalised SST by
272 subtracting the median SST observed across the species' range. This variable transformation
273 improved convergence when fitting and reduced the potential correlation between β_0 and β_1, thereby
274 removing the need to also estimate an additional correlation parameter. A positive estimate for β_1
275 would indicate a positive association between local SST and mean fish length. The α-terms describe
276 random effects due to spatial variation among surveyed cells ($\alpha_{\text{cell}[i]}$, due to e.g. different
277 productivity, human pressure), temporal variation among survey years ($\alpha_{\text{year}[i]}$, due to random
278 variation across years not associated with temperature), and random variation among the surveys
279 themselves (α_i, e.g. observer, site, or weather differences). In this study a 'survey' is treated as a
280 specific day in a given cell and can comprise several 50-m transect surveys. Each of the three α-
281 terms were assumed to be drawn from a normal distribution with zero mean and standard deviation
282 to be estimated (denoted σ_{cell}, σ_{year}, σ_{survey}). To account for the observed fish lengths being
283 necessarily binned we integrated this normal distribution across each of the *K* bin ranges to calculate
284 the probability of fish being observed in each bin. To account for potential outliers in estimated

lengths we also assumed that there was a small probability $\varepsilon = 0.01$ that a fish was observed in a randomly chosen bin. These probabilities form the basis of our likelihood function and Bayesian methods were then used to estimate the six model parameters for each species and assess their uncertainty. Uniform priors were used for all parameters: [1.5–3.5] for β_0, [-0.5–0.5] for β_1, [0.001–1] for σ_{cell} and σ_{survey}, [0.001–1.5] for σ_{year}, and [0.1–0.3] for $\sigma_{lnlength}$. After the first set of analyses the posterior probability density plots were visually inspected for each species, and if the posterior densities were not fully included in the prior value range the priors were adjusted and analyses repeated. Yet, we found that priors had little influence on their posteriors due to large sample sizes. Markov Chain Monte Carlo (MCMC) sampling was run with 3 chains of 1000 iterations each, of which the first 500 were discarded as the burn-in and the last 500 were used to generate posterior probability density ranges. Some species did not converge at these settings and analyses were repeated using 1500 iterations and 1000 burn-in period. Further details and the code can be found at https://github.com/astaaudzi/RLSfishSize. Because μ_i is the log transformed body length, the estimated values of β_1 are converted to relative (or %) change in body length as exp(β_1), where β_1 of e.g. -0.02 corresponds to exp(-0.02) = 0.98 or 2% decrease in body length. Thus β_1 values ranging from -0.2 to 0.2 can be interpreted as proportional change in body length.

Given estimates of the slope of mean body size against SST (β_1) for all species, we then assessed if these slopes were linearly associated with either the thermal affinity of a species or its maximum body-size. Species thermal affinity is defined as the SST at the midpoint of its realised thermal distribution, as described in [21,33] and also often referred to as the Species Temperature Index. For the maximum body size we used the median value of five largest observed body size records, which alleviated potential observation errors in the data sets. We accounted for variation in uncertainty associated with each estimate of β_1 as follows. For each species, we calculated the median and the standard deviation of the posterior for β_1. These standard deviations weighted the influence of each median on the linear regression, which we implemented using a hierarchical mixed-effects model.

311 Again, Bayesian methods were used to estimate the regression coefficients and their associated
312 uncertainty for both linear regressions (Fig. 1). Uniform priors were adopted for the y-intercept and
313 slope ([-0.1–0.1] in both cases) and a uniform prior of [0.01,0.1] was also assumed for the standard
314 deviation describing variation in the β_1 estimates about the fitted regression line (Fig. 1).
315
316 Evidence of local, linear trends in mean body size were based on observations for 105 species at nine
317 long-term monitoring locations [19]. We adopted a model very similar to the one used for the spatial
318 analysis, except we assumed a linear relation of body length to year, rather than SST, and allowed
319 both the y-intercept and the slope to vary across locations. For survey *i* at location *j* the mean of the
320 ln-length distribution of a species is given by:
321
322 $$\mu_{i,j} = \beta_{0,j} + \beta_{1,j} y_i + \alpha_{\mathrm{year}[i]} + \alpha_i,$$
323
324 where y_i and year[i] are the year of the survey described as a covariate and a factor, respectively. The
325 $\beta_{1,j}$ describes long-term temporal change in log-length across locations, which is of specific interest,
326 and the $\alpha_{\mathrm{year}[i]}$ describe stochastic year-to-year changes in length common across locations due to
327 unknown environmental factors. The binning of observed fish lengths was treated in the same way as
328 in spatial analysis. Bayesian methods were again used to estimate the model parameters. Uniform
329 priors were used for all parameters: [1–4] for $\beta_{0,j}$, [-0.1–0.1] for $\beta_{1,j}$, [0.001–0.5] for σ_{year} and
330 σ_{survey}, and [0.1–0.5] for $\sigma_{\mathrm{lnlength}}$. These priors had little influence on the posteriors.
331
332 Five of the long-term locations included observations both inside and outside of no-take marine
333 protected areas (MPA) and we also tested whether temporal trends in body size differed between
334 sites inside and outside MPAs. This was done to assess whether harvesting could be driving temporal
335 trends in observed body sizes. The MPAs are officially no-take areas, and even though small amount
336 of illegal harvesting is likely to occur, the fishing rates are more intense outside MPA areas. The two

337 datasets had 84 and 74 species, respectively, with 69 species found with sufficient abundance both
338 inside and outside MPAs. The overall average body size trends through time were similar inside and
339 outside MPAs (Supplementary Information Fig. 2), suggesting that temporal body size trends were
340 not driven by exploitation. This was not surprising, given that majority of the species analysed (after
341 the filtering described above) are not routinely targeted by commercial or recreational fishing. Final
342 temporal analyses were therefore done on a combined dataset ignoring the MPA effects (105 species
343 across 9 locations).
344
345 To compare rates of body size change across space and time we explored correlation between the
346 body size responses in spatial analyses (β_1) and annual body size trends ($\beta_{1,j}$) at eight locations with
347 significant warming trends. Out of 105 species included in the temporal analyses, 28 species were
348 found only in one non-warming location (Jurien Bay) and were not included in the space-time rate
349 comparison. From the remaining 77 species, six species did not have sufficient spatial data, so the
350 final dataset for the space-time rate comparison included 71 species. For these species correlations
351 between spatial and temporal slopes were assessed using bootstrapped weighted Spearman's
352 correlation (10000 bootstrap replicates), where each value was weighted by the inverse of its
353 uncertainty range (code available at https://github.com/astaaudzi/RLSfishSize).
354
355 Species abundance and therefore potential density dependence effects were not included in the main
356 model, because the relationship describing potential abundance effects on body size are unlikely to
357 be linear, and because competition is likely to occur at both intra- and inter-specific level.
358 Accounting for all these effects would require a very complex, parameter-rich model and much
359 larger datasets that was available for most species. However, to assess whether density dependence
360 could still be the major driver of the observed body trends (if abundance was determined by SST) we
361 compared the species-specific spatial body size slopes (β_1) with abundance-SST skew statistics
362 assessed in [23]. The skew statistics describe relative abundances of a species across its distribution

range, where positive skew means that a species is more abundant at the warmer half of its distribution and vice versa. If abundance was a major driver of average body size, we could expect an overall negative correlation between size-temperature and abundance-temperature slopes, such as mean body size is smaller at sites with higher abundances. Alternatively, larger average body sizes might have positive effects on abundance through e.g. improved recruitment or inter-specific effects. In this case we could expect a positive correlation between size-temperature and abundance-temperature slopes. Estimates of both size-temperature slopes (this study) and abundance-temperature skew [23] were available for 300 species. The correlation between body size slopes and abundances was close to zero ($r = 0.09$, $p = 0.14$), suggesting that abundance is unlikely to be a major driver of body sizes and vice versa (Extended Data Fig. 2).

All statistical analyses were performed using R v.3.2, Bayesian analyses were done using the *rstan* package[34].

Data availability. Underwater visual survey datasets are available through the Reef Life Survey site www.reeflifesurvey.com. The final datasets and all codes used in this analysis are available through the code depository at https://github.com/astaaudzi/RLSfishSize and as Supplementary datasets linked to this article.

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Reporting summary. Further information on experimental design is available in the Nature Research Reporting Summary linked to this paper.

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Author contributions

AA designed the study and led the writing. AA and SAR designed and conducted the statistical analyses. RDSS, GJE and NSB led field surveys and data collection. All authors contributed critically to the development of the study, drafts and gave final approval for publication.

Author information

The authors declare no competing interests. Reprints and permissions information is available at www.nature.com/reprints. Correspondence should be addressed to asta.audzijonute@utas.edu.au

Figure legends

Fig. 1. Relative change in the mean body length of 335 coastal marine fish species per one degree change in SST observed across their geographic distributions. Change varies with species' thermal affinity [21] (A) and maximum observed body length (B). Dots and vertical bars represent the median and 80% PPD ranges of individual species responses, respectively (wide intervals that fall outside the picture limits are not shown). Species that show clear body size responses to SST (90% PPD range above or below zero) are shown in red and blue colours. Solid black line is the linear regression weighted according to the individual species uncertainty level. Orange shading depicts the 95% credible interval for the regression.

Fig. 2. Long-term annual relative change in mean body length of 71 species at eight warming locations. Change through time is positively correlated with the change in mean body length per 1°C SST across their geographic distribution (see Fig. 1). The orange line shows the case where spatial and temporal trends are perfectly correlated but change in body length per 1°C of warming through time is 10 times faster than change per 1°C of warming through space (see text for details). Correlation between spatial and temporal responses was calculated using bootstrapped weighted Spearman's correlation (ρ).

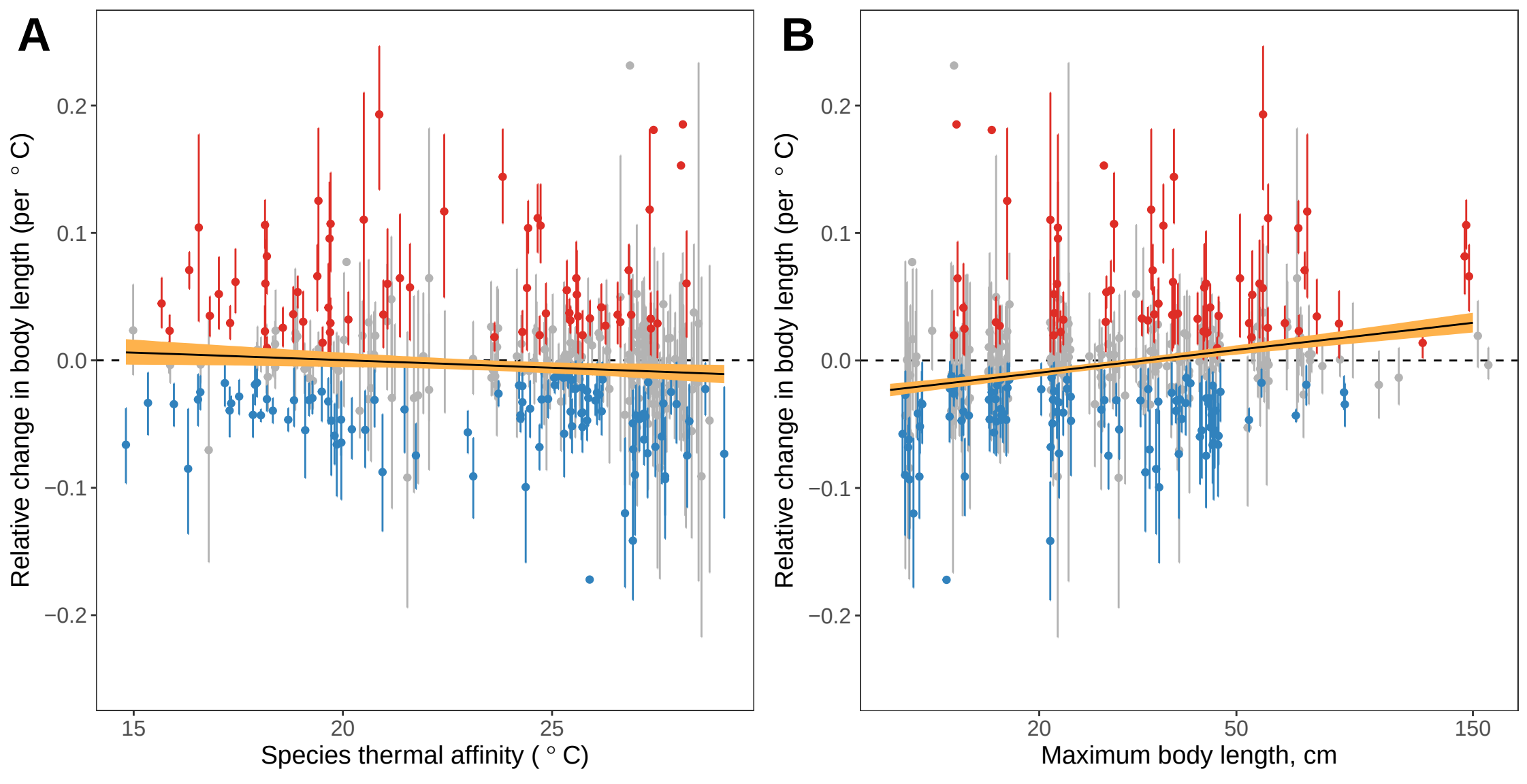
513 **Extended Data Figure Legends**

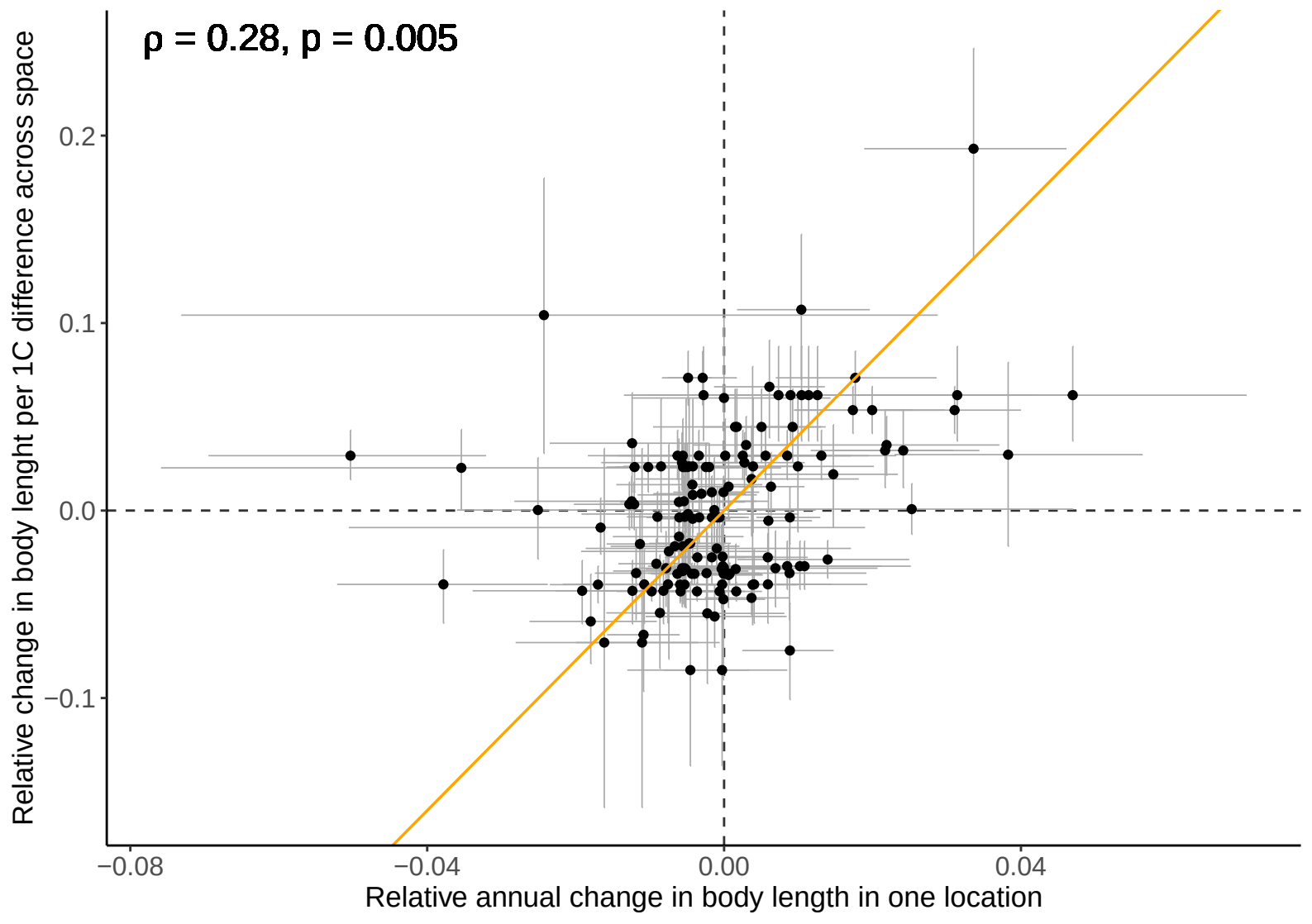
514

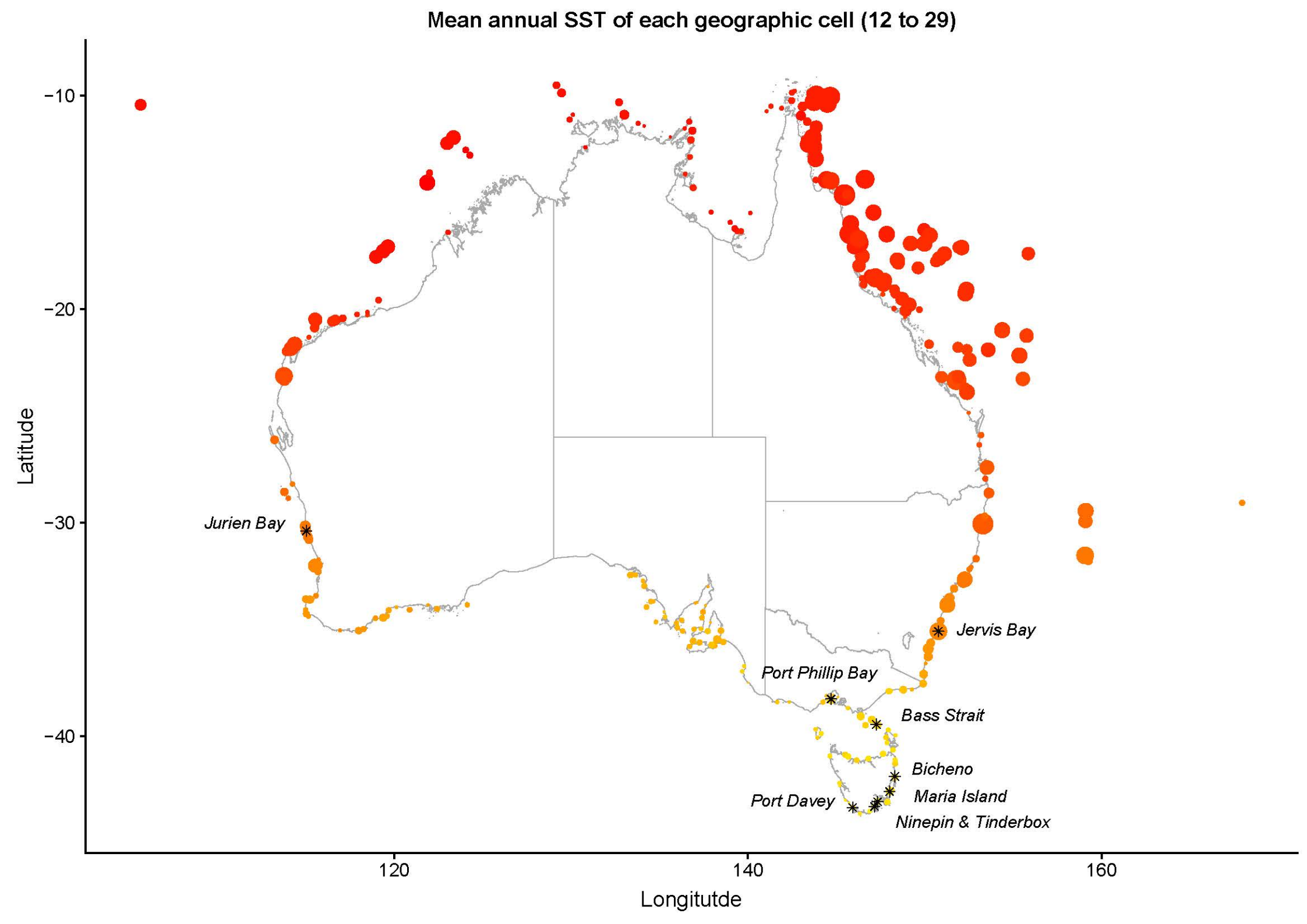
515 **Extended Data Figure 1.** Spatial distribution of Australian fish survey data used coloured according
516 to the mean annual temperature. All sites are grouped onto 0.5 degree grid cells. Colours represent
517 mean annual SST over the entire sampling period in that cell (ranging from 12°C for yellow to 29°C
518 for red) and circle size is proportional to the total number of species used for the analyses in the cell
519 (determined by species richness and number of surveys in the cell). Black stars indicate the nine
520 long-term monitoring locations. The Australian coastline shapefile was downloaded from the
521 Australian Natural Resources Data Library website (Creative Commons (CC) Attribution 3.0
522 Australia licence)

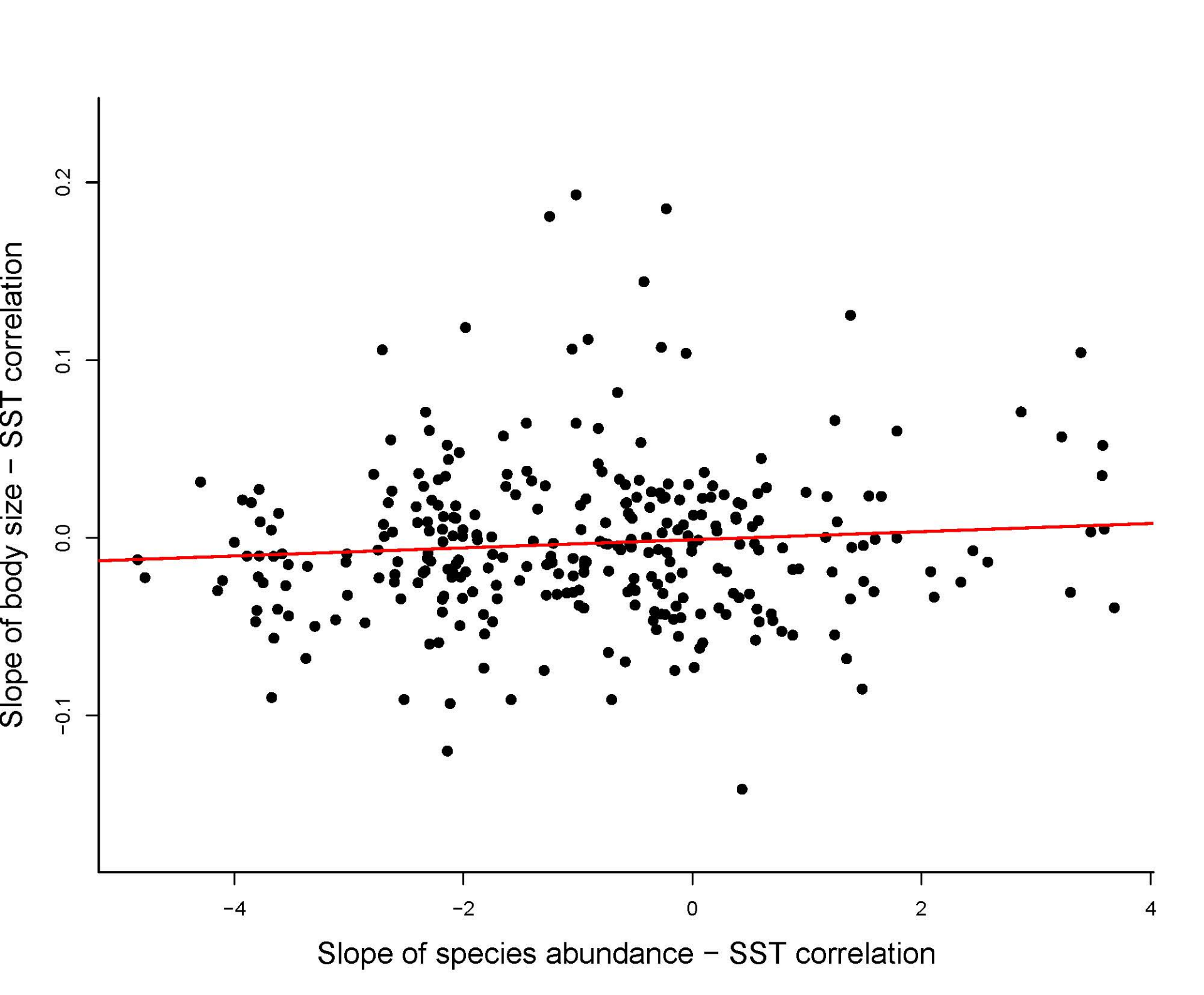
523 **Extended Data Figure 2.** Species-specific slopes between body size and mean annual SST through
524 space (β_1, on y axis) are compared with the species specific abundance and mean annual SST
525 slopes estimated in Waldock et al. (2019). Data on both slopes was available for 300 species. If
526 abundance was a major driver of average body size, we could expect an overall negative correlation
527 between size-temperature and abundance-temperature slopes, such as mean body size is smaller at
528 sites with higher abundances. Alternatively, larger average body sizes might have positive effects on
529 abundance through e.g. improved recruitment or inter-specific effects. In this case we could expect a
530 positive correlation between size-temperature and abundance-temperature slopes. The correlation
531 between body size slopes and abundances was close to zero ($r = 0.09$, $p = 0.14$), suggesting that
532 abundance is unlikely to be a major driver of body sizes and vice versa.

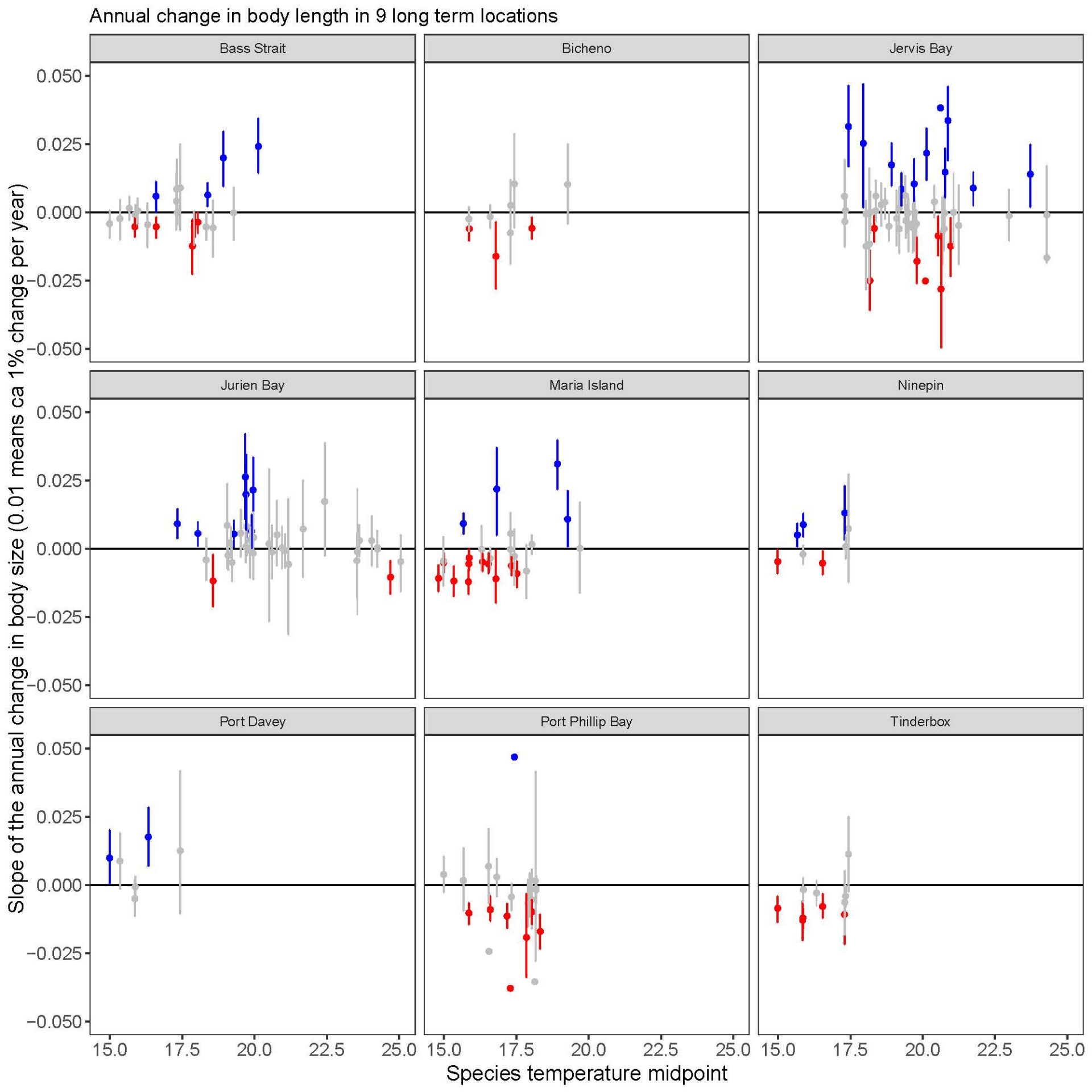
533 **Extended Data Figure 3**. Location and species specific temporal responses, represented by slopes of
534 body length change in 105 coastal fish species in nine warming and long-term monitored locations.
535 Each dot represents a species, arranged according to the temperature at the centre of their distribution
536 area (temperature midpoint). Blue and red colours indicate species for which 90% of the posterior
537 probability density range for the slope of the annual body length change (on y axis) was above or
538 below zero, respectively. For the map of the nine locations see Extended Data Fig. 1.


A
B
Relative change in body length (per ° C)
0.2
0.1
0.0
−0.1
−0.2
15
20
25
Species thermal affinity (° C)
20
50
150
Maximum body length, cm


ρ = 0.28, p = 0.005
Relative change in body lenght per 1C difference across space
0.2
0.1
0.0
−0.1
−0.08
−0.04
0.00
0.04
Relative annual change in body length in one location


Mean annual SST of each geographic cell (12 to 29)
Latitude
−10
−20
−30
−40
120
140
160
Longitutde
Jurien Bay
Jervis Bay
Port Phillip Bay
Bass Strait
Bicheno
Maria Island
Port Davey
Ninepin & Tinderbox


Slope of body size – SST correlation
0.2
0.1
0.0
−0.1
−4
−2
0
2
4
Slope of species abundance − SST correlation


Annual change in body length in 9 long term locations
Bass Strait
Bicheno
Jervis Bay
Jurien Bay
Maria Island
Ninepin
Port Davey
Port Phillip Bay
Tinderbox
0.050
0.025
0.000
−0.025
−0.050
15.0
17.5
20.0
22.5
25.0
Slope of the annual change in body size (0.01 means ca 1% change per year)
Species temperature midpoint

Fish body sizes change with temperature, but not all species shrink with warming

Asta Audzijonyte[1,2], Shane A. Richards[3], Rick D. Stuart-Smith[1], Gretta Pecl[1,2], Graham J. Edgar[1], Neville S. Barrett[1], Nicholas Payne[4] and Julia L. Blanchard[1,2]

Supplementary Information

Supplementary Tables (2-3)

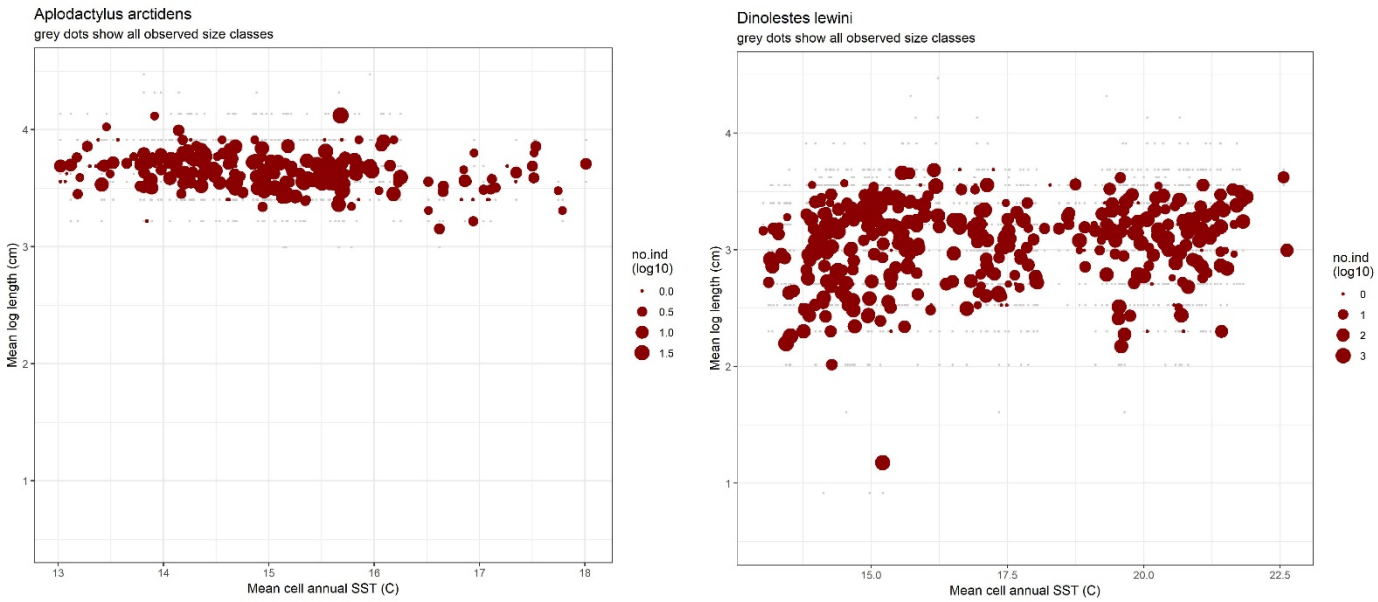
Supplementary Figures (1-3)

Supplementary Table 2. Summary of body length trends across space (335 species classified as temperate or tropical) and time (156 observations of 77 species in eight warming locations). For each group, the proportion (*prop*) of species with positive and negative body length responses to temperature are shown for all species and for the species that are deemed to have significant change (lower or upper 10% of PPD ranges don't overlap with zero). Median change (*median*) in body length per 1 ^{o}C SST change is also shown for each category. *SST range* shows a median value for difference between minimum and maximum mean annual SST values (^{o}C) across species distribution ranges (note, this is not the minimum or maximum SST ever recorded in the range, but minimum and maximum of annual means). A similar range for all groups (ca 8^{o}C) shows that tropical species on average do not live in a narrower range of temperature conditions across their distribution areas, compared to the temperate species. *Length* is the median observed length. The second column in the table shows either the number of species (*spp*, for spatial analyses), or both species and species x location combinations (for temporal analyses) (see Extended Data Table 3). The number of increasing or decreasing rates in the temporal analyses are shown for species x location combinations (i.e. proportions are compared to the 156 and 66 speciesxlocations and not 77 and 40 species).

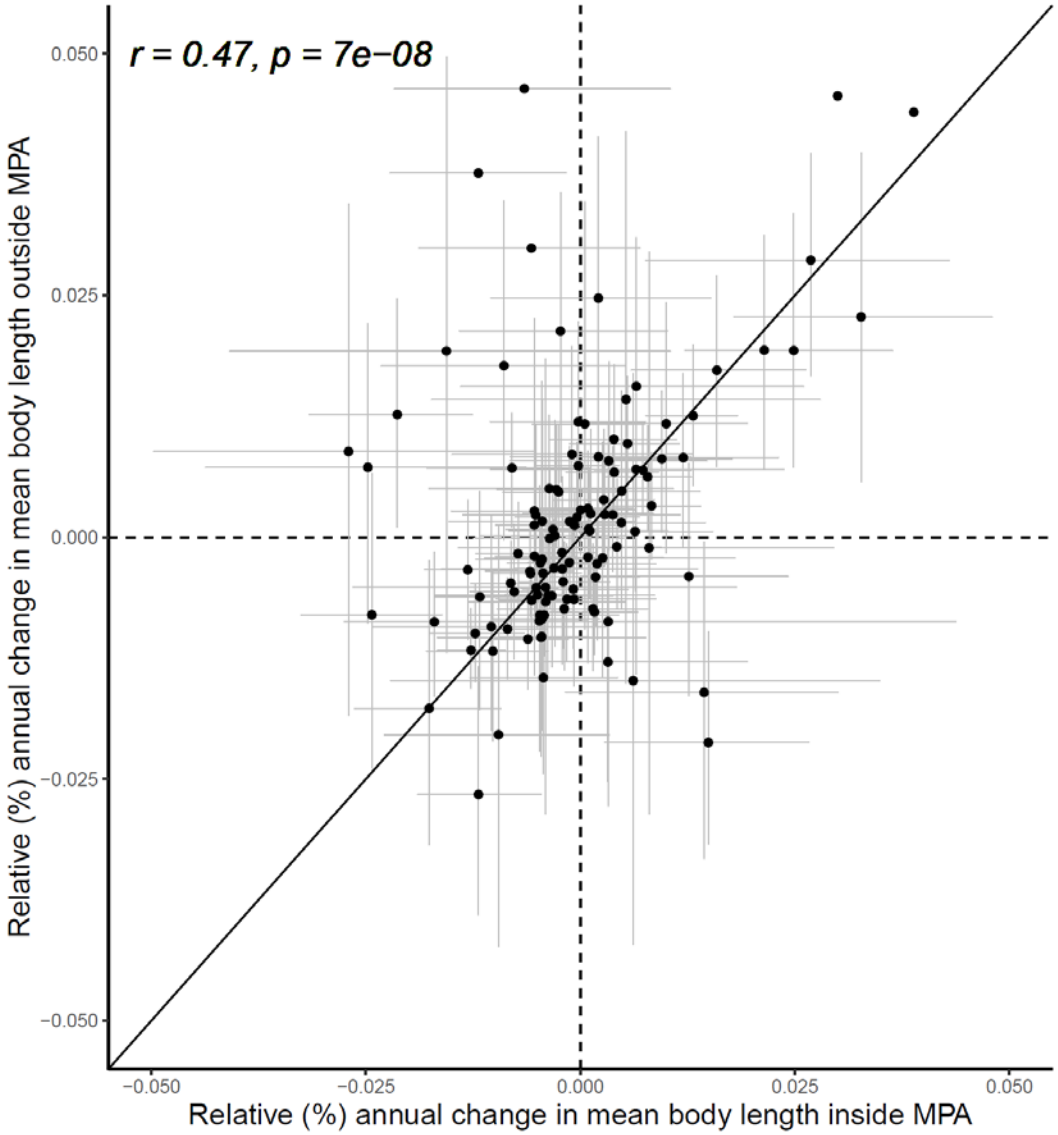
Thermal guild	***spp / spp x loc***	**increasing (slope > 0)** ***no/prop***	***median***	**decreasing (slope < 0)** ***no/prop***	***median***	***SST range,*** ^{o}C	***Length,*** cm
Body length changes per 1 ^{o}C SST change through space							
Tropical species		***per 1 ^{o}C SST***		***per 1 ^{o}C SST***			
All species	218	88 / 0.40	2.2%	130 / 0.60	2.3%	7.9	10.0
Sign. change	93	31 / 0.33	3.7%	62/ 0.67	4.0%	8.1	9.2
Temperate							
All species	116	57 / 0.49	3.0%	59 / 0.51	3.1%	7.6	15.0
Sign. change	68	33 / 0.49	5.4%	35 / 0.51	3.9%	7.7	15.9
Body length changes per year at eight warming locations							
Temperate		***per year***		***per year***			
All species	77/156	56 / 0.36	0.85%	100 / 0.64	0.53%		
Sign. change	40/66	25 / 0.38	1.5%	41 / 0.62	1.0%		

Supplementary Table 3. Slopes and 80% PPD ranges annual temperature trends for the nine locations, ranked from least warming to fastest warming. NSt – total number of ATRC and RLS sites, β_1 – slope of temperature change per year (median, 10% and 90% of PPD distribution), *No. spp* indicates the number of species in the location for the temporal analyses, Incr – number of species increasing in body size (90% PPD range for slope above zero), Decr – number of decreasing species (90% PPD range for slope below zero), and % changing shows the percentage of species that are increasing or decreasing in body size at a location based on the criteria above. Location names are shown on Extended Data Fig. 1.

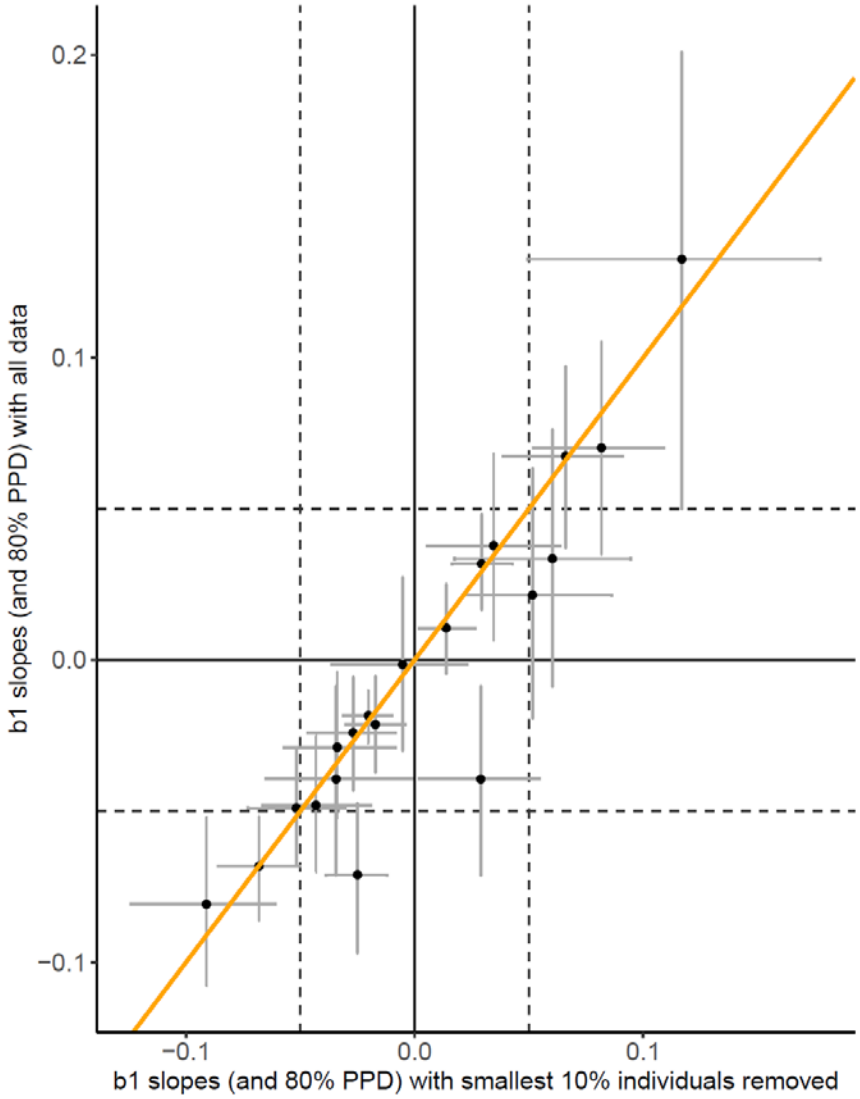
Location	NSt	$\beta_{1,\,median}$	$\beta_{1,10\%}$	$\beta_{1,90\%}$	No. spp	Incr	Decr	%
Jurien Bay (WA)	50	0.009	0.005	0.013	36	7	2	25
Bass Strait	37	0.023	0.019	0.026	23	4	5	39
Port Phillip Bay (VIC)	89	0.023	0.020	0.026	22	1	7	37
Port Davey (TAS)	54	0.024	0.019	0.028	7	2	1	43
Bicheno (TAS)	18	0.027	0.023	0.031	9	0	3	33
Ninepin (TAS)	14	0.027	0.024	0.031	8	3	2	63
Tinderbox (TAS)	9	0.027	0.024	0.032	10	0	5	50
Maria Island (TAS)	32	0.029	0.025	0.033	24	4	11	63
Jervis Bay (NSW)	93	0.037	0.033	0.043	53	11	7	34



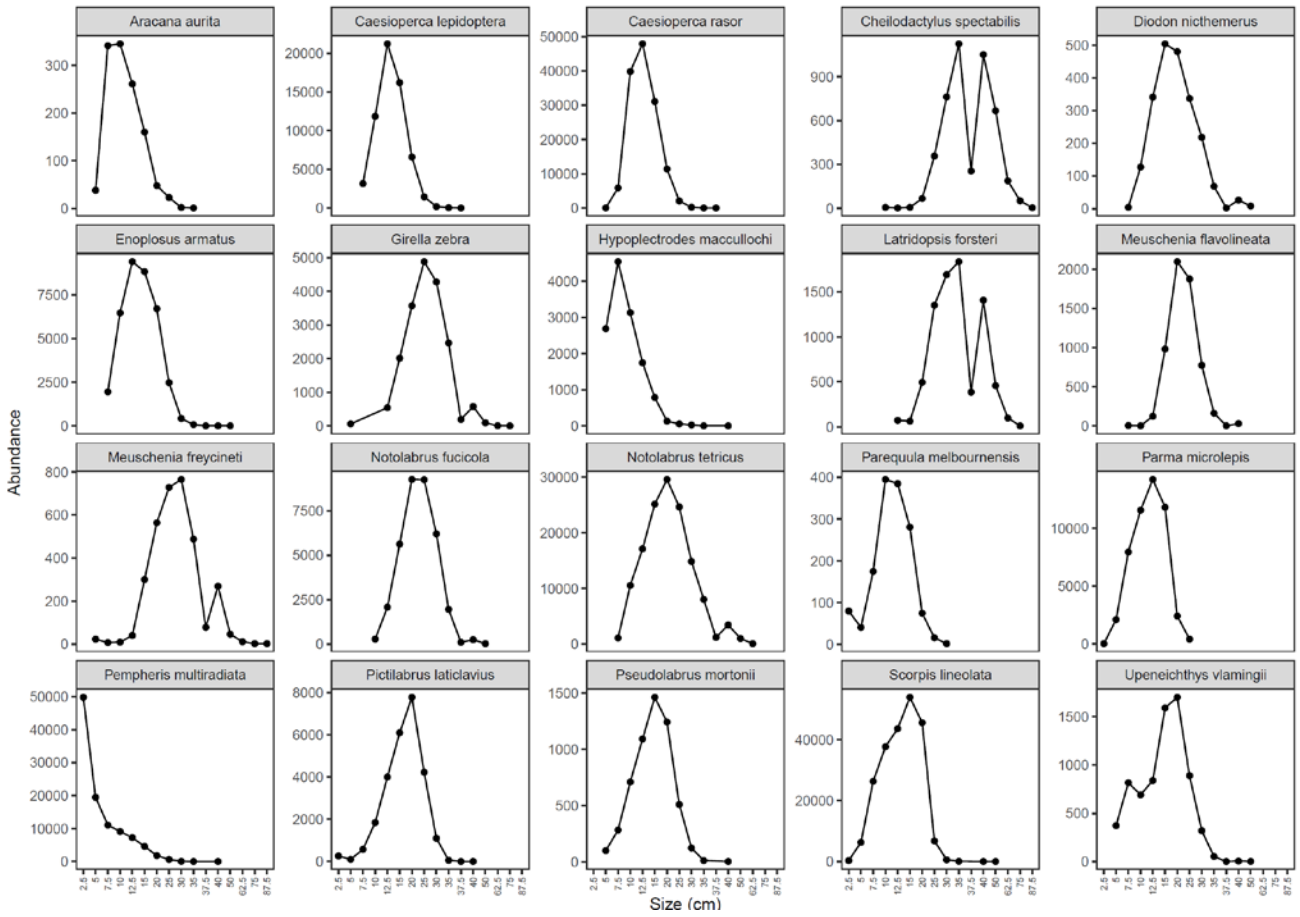
Supplementary Figure 1. Distributions of species body sizes against the annual SST values in the 280 geographic cells. Mean body size and mean SST values are calculated for each year and each cell separately. These plots were inspected to assess for outlier observations, indicating possible identification errors, and to assess the quality of data. Two example plots are shown for species with a significantly positive (*Dinolestes lewini*) and negative (*Aplodactylus arctidens*) body size responses to SST. Plots for all 335 species through space and for the 77 species through time can be found on https://github.com/astaaudzi/RLSfishSize/



Supplementary Figure 2. Estimated slopes of annual changes in body length inside and outside no-take marine protected areas. The 50% posterior density probability shown with dots, and 80% PPD range as grey lines; data is shown for 69 fish species from 121 species x location combinations. The Pearson correlation is shown on the left top corner. Solid black line depicts a 1:1 correlation.



Supplementary Figure 3. Assessment whether excluding the smallest 10% of individuals is likely to affect estimates of body size – temperature correlations through space. Correlation between β_1 slope estimates for 20 small and large species from data used in the main analysis (with lower 10% of body sizes removed to exclude effects of recruitment pulses) and with all data. The estimated 10%, 50% and 90% PPD values of slope between β_1 and maximum body size depicted by the orange line in Fig.2A was 0.0115, 0.0183 and 0.0247 for the analyses where the 20 species were replaced with full data, and 0.0133, 0.0194 and 0.0259 for the original analyses. The error bars show 80% PPD ranges for the two sets of estimates, dots show the median value. The orange line indicates a perfect 1:1 fit. Further details about the test and the species used for the analyses are on https://github.com/astaaudzi/RLSfishSize/



Supplementary Figure 4. Size distributions in the first 20 fish species from the dataset, showing that distributions approximately follow log-normal distribution. To explore size distributions of all other species in the data set, use the supplementary code provided at https://github.com/astaaudzi/RLSfishSize/.